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Affiliation of *Hyostrongylus rubidus* (Nematoda: Trichostrongylidae) with the Ostertagiinae, and Evaluation of the Synlophe and Other Structural Characters

E. P. HOBERG, J. R. LICHTENFELS, AND P. A. PILITT
United States Department of Agriculture, Agricultural Research Service, Biosystematic Parasitology Laboratory, BARC East No. 1180, 10300 Baltimore Avenue, Beltsville, Maryland 20705-2350

ABSTRACT: Classifications of the Trichostrongylidae have referred *Hyostrongylus* Hall, 1921, to the Ostertagiinae or the Graphidiinae. The genital cone and synlophe of *Hyostrongylus rubidus* (Hassall and Stiles, 1892) were studied to clarify the subfamilial position of the genus and to assess hypotheses for the origin of the Ostertagiinae. Paired "0" papillae, a putative synapomorphy for the Ostertagiinae, are located on the ventral aspect of the genital cone in *H. rubidus*. This character, along with the structure of the bursa, confirmed placement of *Hyostrongylus* in the Ostertagiinae rather than the Graphidiinae. The synlophe was composed of a largely symmetrical system of continuous ridges extending from the cervical zone to near the caudal extremity in males and females. At the midbody there were 40–58 ridges; in females the vulval region was modified by irregular cuticular inflations. It was concluded that current concepts for independent origins of genera of the Ostertagiinae from the Graphidiinae were not supportable, as such would result in polyphyly for the former and paraphyly for the latter subfamily. Additionally, the genus *Cervicaprastrongylus* Gibbons and Khalil, 1982, was considered to be distinct from *Hyostrongylus*.

KEY WORDS: Trichostrongylidae, *Hyostrongylus*, Ostertagiinae, Graphidiinae, synlophe, genital cone.

Hyostrongylus rubidus (Hassall and Stiles, 1892) Hall, 1921, the type for the genus (synonyms: *Strongylus rubidus* Hassall and Stiles, 1892; *Ostertagia rubida* Travassos, 1918; *Haemonchus rubidus* Sluiter and Swellengrebel, 1912; and *Trichostrongylus rubidus* Fiebeger, 1923) was originally recognized as a nematode parasite of the white-lipped peccary (*Tayassu pecari* (Link) = *Dicotyles albirostris* Illiger) in Brazil. Later described from domestic swine (*Sus scrofa* Linnaeus), it is now recognized as a characteristic parasite of the Suidae and Tayassuidae (Molin, 1860; Hassall and Stiles, 1892; Levine, 1980).

Hyostrongylus rubidus is considered as a cosmopolitan parasite of domestic swine and other suids and has been rarely reported from ruminants or other herbivores (Levine, 1980). The nematode is essentially absent in sylvatic ruminants from sub-Saharan Africa (Round, 1968) and has only recently been reported from bush pigs (*Potamochoerus porcus* (Linnaeus)) and red duikers (*Cephalophus natalensis* Smith) in South Africa (Boomker, 1990; Boomker et al., 1991). There are apparently only 3 records from cattle (South America, The Netherlands, Ukraine) and 2 from sheep (North America, Ukraine) (Becklund and Walker, 1967; Da Costa and Benevenga, 1971; Borgsteede, 1978; Levine, 1980; Trach, 1986). Roe deer (*Capreolus capreolus* (Linnaeus)) in Bulgaria have been the only cervids recognized as hosts (Ianchev, 1973). Records from lagomorphs are limited to European hares (*Lepus capensis* Linnaeus; reported as *L. europaeus*) in Austria (Kutzer and Frey, 1976).

Although the genus *Hyostrongylus* Hall, 1921, was established for *H. rubidus* from swine (Hall, 1921), Travassos (1921) referred this species to *Ostertagia* Ransom, 1907. Goodey (1924), Alicata (1935), and Travassos (1937) considered *Hyostrongylus* to be valid, as the latter author relegated the genus to the subfamily Trichostrongylinae. Possible affinities to *Ostertagia* and related genera were again indicated by the decision of Skrjabin and Shul'ts (1937; cited *in* Skrjabin et al., 1954) to place *Hyostrongylus* in the tribe Ostertagiea of the subfamily Trichostrongylinae. However, the tribe Hyostrongylea was later established for *H. rubidus* and several other genera within the Cooperiinae (Skrjabin et al., 1954). Subsequently, *Hyostrongylus* was transferred to the Graphidiinae by Durette-Desset and Chabaud (1977, 1981) and since has been retained in this subfamily (Durette-Desset, 1982, 1983, 1985, 1989). In contrast, Gibbons and Khalil (1982a) and Jansen (1989) supported recognition of *Hyostrongylus* within the Ostertagiinae, and Trach (1986) referred the tribe Hyostrongylini with *H. rubidus* to this subfamily.

Nematodes of this genus have been considered to hold an intermediate position with respect to

these latter subfamilies (Durette-Desset and Chabaud, 1977, 1981; Jansen, 1989) and, as a consequence, have been referred in recent literature to either the Graphidiinae (Durette-Desset, 1982, 1983, 1985, 1989) or the Ostertagiinae (Khalil and Gibbons, 1981; Gibbons and Khalil, 1982a, b). Thus, the systematics of the genus *Hyostrongylus* remains problematic but must be clarified to promote examination of hypotheses for the evolution of the subfamilies Graphidiinae and the Ostertagiinae of the family Trichostrongylidae (see Durette-Desset and Chabaud, 1977, 1981). Placement of the genus *Hyostrongylus* has a bearing on concepts for the validity and relationships of the Ostertagiinae and the Graphidiinae (Hoberg and Lichtenfels, 1992).

In the present study, we provide a detailed description of the synlophe and genital cone of *H. rubidus* that augments studies by Trach (1986). These data promote an assessment of the subfamilial placement of *Hyostrongylus.* Initial character analysis of the synlophe and genital cone, requisite for phylogenetic studies (Hennig, 1966; Wiley, 1981) among the trichostrongylid subfamilies, was conducted. Synapomorphic characters for definition of the Ostertagiinae were identified and constitute the basis for evaluating previous hypotheses for the relationship of the Ostertagiinae and the Graphidiinae. Comments on the validity of the genus *Cervicaprastrongylus* Gibbons and Khalil, 1982 (a putative synonym of *Hyostrongylus* according to Jansen [1989] and Durette-Desset et al. [1992]) are presented. Additionally, a lectotype, allolectotype, and paralectotypes are designated for *H. rubidus,* as Hassall and Stiles (1892) did not formally select and deposit a holotype and allotype in the original description.

Materials and Methods

Specimens were studied as temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol), or in glycerine, and examined with differential interference contrast light microscopy. Transverse sections were prepared freehand with a cataract knife and embedded in glycerine jelly. Sections were used to study the structure of the synlophe in the cervical zone (including the region of the esophageal–intestinal [EI] junction), anterior quarter, midbody, and posterior region of 6 males (sections prepared to the level proximal to the spicules) and 5 females. The configuration of irregular cuticular inflations at the level of the vulva in females was evaluated in whole mounts and sectioned specimens. Photographs of sections were oriented with dorsal surface toward the top of the plate and shown as if viewed from the anterior. Throughout the manuscript, measurements are presented in micrometers unless specified otherwise and presented as a range with $\bar{x} \pm 1$ SD in parentheses.

The current study focused on the configuration of the synlophe, esophageal valve, and genital cone (following Lichtenfels and Pilitt, 1991; Hoberg et al., 1993a). Other mensural and structural characters are included in the redescription (measurements of the ovejectors follow Lichtenfels and Pilitt, 1991). Genital papillae and bursal rays are numbered according to the methodology developed by Chabaud et al. (1970), and the orientation of the synlophe follows concepts presented by Durette-Desset (1985). The term "cuticular strut" follows Lee (1965).

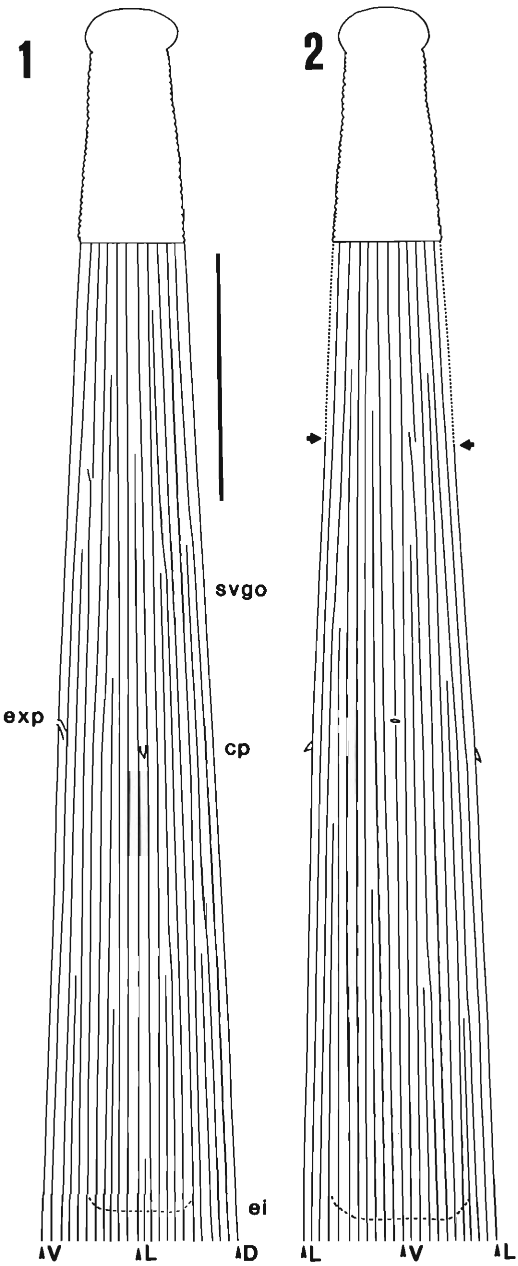
Specimens Examined

Specimens were obtained from the U.S. National Parasite Collection maintained at the Biosystematic Parasitology Laboratory, United States Department of Agriculture, Beltsville, Maryland, and included material from a variety of locations in North America and Central America collected between 1892 and 1981 (Table 1). Hassall and Stiles (1892) did not formally designate a holotype and allotype in the original description and such were not indicated among the specimens denoted as syntypes (USNM No. 14). Consequently a male specimen from this lot was selected as the lectotype and a female as the allolectotype for *Hyostrongylus rubidus,* with the remaining male and female syntypes becoming paralectotypes in accordance with the third edition of the International Code of Zoological Nomenclature (1985).

Results

General characters (synlophe and esophagus)

The synlophe in *Hyostrongylus rubidus* is composed of a largely symmetrical system of continuous parallel cuticular ridges that extends from the base of the cephalic expansion to near the caudal extremity in males and females (Figs. 1, 2). Ridges are perpendicular to the body wall, and a gradient or orientation is absent. In the cervical zone (anterior to the base of the esophagus), 18–22 ridges attain the base of the cephalic expansion. There are 34–42 and 32–44 ridges at the level of the prominent, thorn-like cervical papillae in males and females, respectively. Variation in numbers is attributable to differences in the levels of origin for individual ridges in the anterior. At the limit of the EI junction, there are 38–50 ridges in males and 42–55 in females. The synlophe is of uniform height, and there is minimal variation in the interval between ridges, as determined from sections, laterally, ventrally, or dorsally. A slight dorsoventral asymmetry is evident in the numbers of ridges posterior to the



Figures 1, 2. Cervical synlophe of *Hyostrongylus rubidus*. Scale bar = 100 μm. 1. Typical male specimen showing left lateral view and pattern of evenly spaced parallel ridges. Note the 2 pairs of continuous ridges that border the lateralmost ridge (L) and the anterior position of the subventral gland orifices (svgo). Other attributes depicted include the ventral (V) and dorsal (D) ridges, excretory pore (exp), cervical papilla (cp), and esophageal–intestinal junction (ei). 2. Male specimen showing ventral view and pattern of parallel ridges. Note that the lateral ridges (L) do not extend to the base of the cephalic expansion (indicated by dotted lines and arrows to denote region of termination). There are 3 continuous ventral ridges (similar to the Type A ventral system defined by Lichtenfels et al. [1988]) and the ventral ridge is interrupted at the level of the excretory pore.

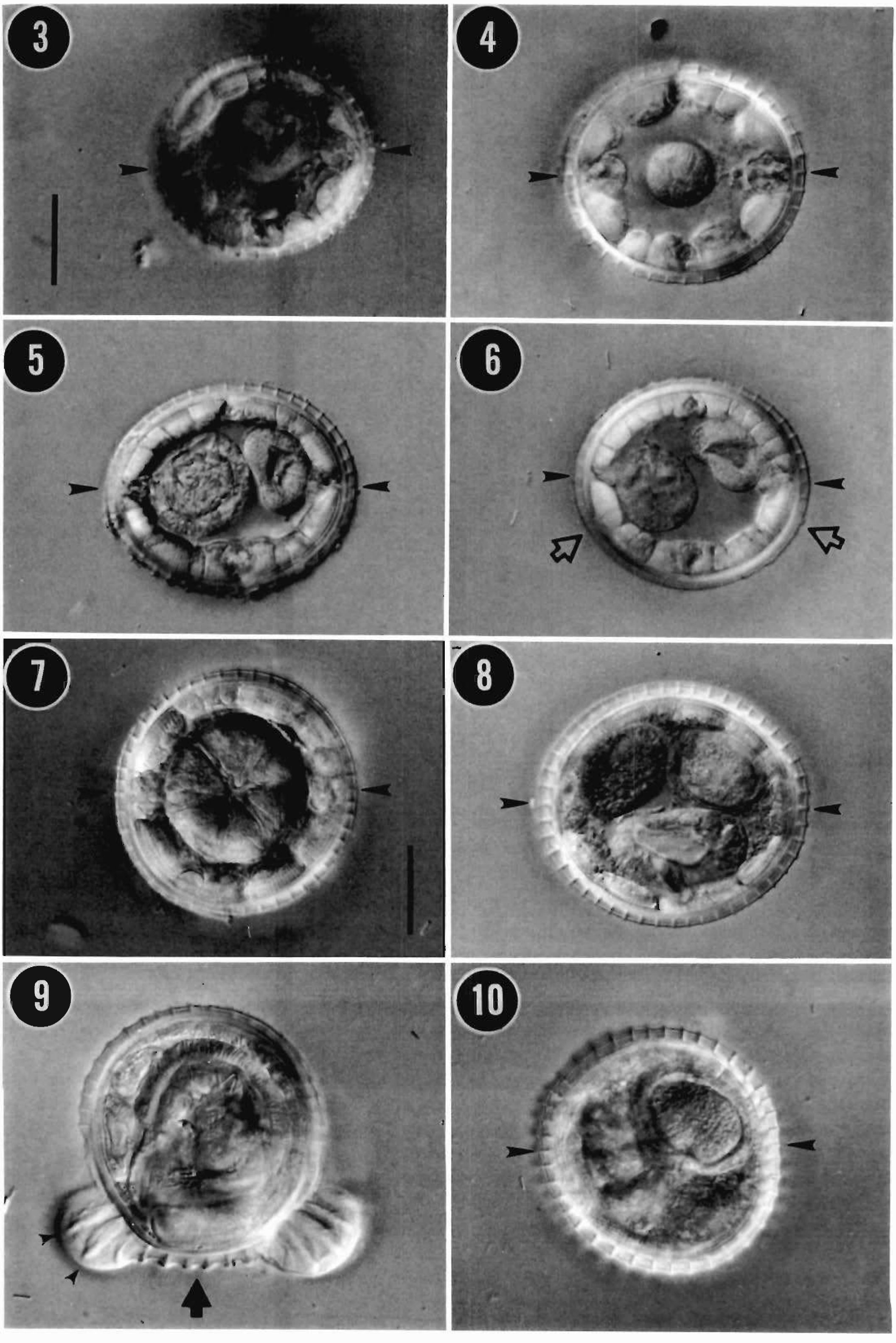
Table 1. List of specimens of *Hyostrongylus rubidus* with hosts and geographic localities.

USNM No.*	Locality	Host	♂†	♀†
82538‡	Maryland	*Sus scrofa*‖	1	1
14§	Maryland	*Sus scrofa*‖	6	5
5355	Maryland	*Sus scrofa*‖	2	1
18136	Virginia**	*Sus scrofa*‖	2	0
24540	Virginia	*Sus scrofa*‖	6	3
26226	Iowa	*Sus scrofa*‖	2	0
29398	Louisiana	*Sus scrofa*‖	5	5
31457	Puerto Rico	*Sus scrofa*‖	4	5
32649	Florida	*Sus scrofa*‖	6	4
56796	Illinois	*Ovis aries*‖	1	3
58403	Panama	*Sus scrofa*‖	6	6
61117	Maryland	*Sus scrofa*‖	11	12
68480	Maryland	*Sus scrofa*‖	11	12
69787	Alabama	*Sus scrofa*‖	5	5
76758	Florida	*Sus scrofa*††	3	3

* Collection number from U.S. National Parasite Collection.
† Numbers of specimens examined.
‡ Designated lectotype and allolectotype, selected from syntypes examined by Hassall and Stiles (1892).
§ Paralectotypes, representing remaining syntypes from Hassall and Stiles (1892).
‖ Domestic hosts.
** Animals originated in Kansas.
†† Sylvatic hosts.

cervical papillae, where often 1–2 unpaired ridges are present in either the dorsal or ventral fields.

Laterally, 2 pairs of continuous ridges bordering the lateralmost ridges (Fig. 1) extend from the cephalic expansion usually to near the caudal extremity, resulting in 5-ridge lateral fields (lacking a narrow interval between ridges, and not definable as the Type II pattern of Lichtenfels et al. [1988, 1990]). The left and right lateralmost ridges extend <75% of the distance anterior from the cervical papillae to the cephalic expansion and are slightly smaller than those in the adjacent lateral fields (Figs. 1, 2). Origins of ridges ventral and dorsal to these lateral fields usually occur adjacent to the 5-ridge system. However, single ridges may originate directly adjacent to the lateralmost near or posterior to the base of the esophagus and only rarely in the region near the cervical papilla. Ventrally in the cervical zone there are 3 continuous parallel ridges (Fig. 2) with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the ventralmost being interrupted at the excretory pore (similar to the Type A pattern of Lichtenfels et al. [1988]).

Posterior to the cervical zone there is considerable variation in the numbers of ridges and extent of the synlophe in males and females (Figs. 3–10). Ridges may originate in the lateral, dorsal, or ventral fields. Among males there are 41–57 ridges at the end of the first quarter, generally increasing to 40–58 at the midbody (Fig. 4). Posterior to the midbody there is sequential loss of ridges (Fig. 6), with the synlophe terminating dorsally at 67–96% of the body length from the anterior, ventrally at 65–92%, and laterally at 67–98% (prebursal papillae are situated at approximately 98% from the anterior); posteriad extent of the synlophe is not correlated with total length of the nematode. Consistently, the synlophe extends further posteriad laterally and dorsally than ventrally (Fig. 6). Although the synlophe may occasionally extend to near the prebursal papillae, usually prominent ventral and dorsal arcuate gaps are evident in the posterior third of the body. The interval between lateral ridges remains relatively constant; however, spacing of the dorsal and ventral ridges increases posteriad, coinciding with the termination of the synlophe. In contrast, among females there are 50–55 ridges at the end of the first quarter, 43–56 at the midbody (Fig. 8), 45–55 in the posterior third quarter, and 41–49 near the point of termination adjacent to the anus (Fig. 10); some lateral and dorsal ridges may extend onto the tail. Modification of the synlophe occurs at the level of the vulva where ridges may be interrupted ventrally and/or hypertrophied to form irregular cuticular inflations (Fig. 9), described in detail later. In females the interval among the lateral, ventral, and dorsal ridges remains relatively constant until termination of the synlophe near the anus.

The EI valve is relatively short in males and females (55–86 μm) (Tables 2, 3; Fig. 11). The orifices of the subventral esophageal glands are usually substantially anterior to both the cervical papillae and the excretory pore (Tables 2, 3; Fig. 1). A minuscule, triangular, dorsal esophageal tooth is present.

Female characters

Specimens with a synlophe and esophageal structures identical to those found in males were considered to represent *H. rubidus*. The tail varied considerably in length (Table 3), and consistently several prominent annulations were present (Fig. 12). Modification of the cuticle at the level of the vulva was variable in extent (Figs. 13–15), with inflations, as described later, being the most common ornamentation. However, flaplike structures that slightly overlapped the vulva were observed in 3 of 50 specimens (Fig. 16). The anterior infundibulum and vestibule + sphincter were consistently longer than those in the posterior (Fig. 17).

Among specimens examined (32 of 50), 64% exhibited irregular cuticular inflations at the level of the vulva (Figs. 9, 14, 15). The extent of the inflations was variable, with the most common form being a single broadened ventral zone immediately posterior to the vulva. However, additional prominent inflations occurred ventrally, anterior to the vulva, and as paired or single zones ventrolateral in position (Figs. 14, 15). Inflations are associated with irregular hypertrophy of the synlophe but lack specific orientation, form, or symmetry. Inflations are supported by single or multiple systems of enlarged ridges (fusion of ridges is occasionally observed), with erratically formed struts providing some internal foundation (Fig. 9). However, ridges are not evident superficially on the surface cuticle of most inflations. Posterior to the vulval region, the synlophe regains a typical configuration, as already described (Fig. 10).

Male characters

The bursal ray formula is 2–2–1 (see Durette-Desset, 1983) with the tips of rays 2 and 3 being

←

Figures 3–10. Synlophe of a male and female of *Hyostrongylus rubidus* in transverse section shown as viewed from the anterior with dorsal oriented toward the top of the figure and lateral ridges indicated by pointers. Scale bars = 25 μm. 3–6. Male specimen. 3. Level of esophageal–intestinal junction showing 39 ridges. 4. Midbody, showing 40 ridges. 5. Posterior region of third quarter showing 42 ridges. 6. Anterior region of fourth quarter showing approximately 33 ridges; note absence of ridges across ventral aspect (between arrows). 7–10. Female specimen. 7. Level of esophageal–intestinal junction showing 48 ridges. 8. Midbody showing 48 ridges. 9. Level of vulva (arrow) showing prominent inflations supported by irregularly hypertrophied cuticular struts (small pointers). 10. Posterior region of fourth quarter anterior to the anus showing 41 ridges.

Table 2. Morphometrics (in micrometers; range with $\bar{x}$ and SD in parentheses) of males of *Hyostrongylus rubidus*.*

Characters	1	2	3	4	5	6	7		8		
Number examined	—	—	—	—	—	—	20			50	
Body length	5,000	4,400–5,000	5,000–7,000	3,800–4,900	3,400–5,000	4,000–7,000	5,479–6,929	(6,130)	[49]†	3,047–7,025	(5,608 ± 863.9)
Cephalic vesicle length	—	—	—	—	—	—	—		[47]	60–88	(70 ± 6.76)
Esophagus length	—	—	—	524–539	570–590	—	590–768	(668)	[48]	484–750	(637 ± 50.19)
Esophagus as % of body length	—	—	—	11.0–13.8‡	12–17‡	—	10.7–11‡	(10.9)	[47]	8.9–16	(11.5 ± 1.47)
Esophageal–intestinal valve length	—	—	—	—	—	—	—	—	[49]	55–78	(68 ± 6.31)
Esophageal–intestinal valve width	—	—	—	—	—	—	—	—	[48]	36–57	(45 ± 5.29)
Subventral esophageal gland orifices§	—	—	—	—	—	—	—	—	[45]	186–305	(263 ± 24.5)
Excretory pore§	—	—	—	258–281	209–323	—	219–344	(277)	[46]	252–398	(321 ± 36.78)
Cervical papillae§	—	—	400	273–281	320–360	—	221–367	(290)	[48]	268–433	(339 ± 37.98)
Spicule length‖	130	127–134	—	114–121	127–139	127–134	123–140	(134)	[49]	103–144	(125 ± 9.53)

* 1 = Hassall and Stiles (1892), original description from natural infections in *Sus scrofa* from Washington, D.C. 2 = Travassos (1921), redescription of specimens in *Sus scrofa* from Brazil. 3 = Goodey (1924), redescription of specimens from naturally infected *Sus scrofa* from Great Britain. 4 = Alicata (1935), specimens from experimental infection in guinea pig (*Cavia porcellus*). 5 = Skrjabin et al. (1954). 6 = Sprehn (1957). 7 = Sarashina and Taniyama (1986), redescription from naturally infected *Sus scrofa* in Hokkaido, Japan. 8 = Present study, redescription from natural infections in *Sus scrofa* and *Ovis aries* from North America and Central America.

† *n* for individual measurements.

‡ Calculated from numerical values in previous description.

§ Measured from anterior.

‖ Typically the right and left spicules are equal in length.

convergent. The genital cone is typical of the Ostertagiinae (Fig. 18). The ventral of "0" papillae are paired (Fig. 19) and located on the ventral portion of the genital cone. The accessory bursal membrane is small and rectangular, positioned transversely on the dorsal aspect of the genital cone and supported by widely separated, minuscule "7" papillae (Figs. 18, 20). The dorsal ray (rays 9/10) is 39–47 μm in length, with a pair of large processes at 50–63% of the ray length from the anterior and a diminutive pair of lateral processes slightly anterior to the terminal bifurcation at about 80% from the anterior; additional small processes arise from the tips posterior to the bifurcation (Fig. 21). The dorsal ray is situated ventrally with reference to the externodorsal rays (ray 8) and contained in a small lobe (Figs. 21, 22).

The spicules are relatively short and not of great complexity (Fig. 23). Single dorsal and ventral processes of unequal length originate from the respective ala at 50–60% of the spicule length from the anterior. The dorsal process is long and slender, extending to near the tip of the main shaft (Figs. 18, 22, 23); the obscure ventral process is short and does not approach the spicule tip. The primary shaft of each spicule tip has an obscure hyaline foot and is surrounded by a membrane (Figs. 18, 21). The gubernaculum, highly elongate and narrow, is located dorsal to the lateral plates of telamon (Fig. 18).

Discussion

Morphology of *Hyostrongylus rubidus*

The synlophe in males and females was found to be largely identical, consisting of 38–55 continuous parallel ridges at the level of the EI junction. The numbers of ridges were found to increase posteriad and usually attained a maximum of 40–58 near the midbody. Although the synlophe had not been previously evaluated in detail, Hassall and Stiles (1892) noted 40–45 "longitudinal striae" in the original description of nematodes from North America but did not indicate at what level the ridges were counted. Goodey (1924), Skrjabin et al. (1954), and Thoonen and Vercruysse (1951) also reported the occurrence of ridges but did not specify the number present on specimens from Europe. Durette-Desset et al. (1992) reported approximately 50 indistinct ridges near the level of the midbody in specimens from North America. Sarashina and Taniyama (1986) indicated the presence of 40–45 ridges in specimens from Hokkaido, Japan.

There was a general agreement in morphometrics of most diagnostic characters among specimens representing populations from Asia, Europe, Central America, and North America (see Tables 2, 3). The results of the current study indicate a broader range in the length of the spicules in males and in the tail of females, but other mensural characters did not differ substantially. The spicules in males examined during the current study were found to be trifurcate (dorsal and ventral processes arising from the main shaft), agreeing with recent redescriptions presented in Trach (1986) and Govorka et al. (1988). However, males of *H. rubidus* were previously considered to have relatively unmodified spicules each with a single elongate dorsal process (see Hall, 1921; Skrjabin et al., 1954; Gibbons and Khalil, 1982a). Additionally, irregular vulval inflations in females appear to have been a variable character among most populations of *H. rubidus* examined in the current study. Inflations are rare among congeners (Durette-Desset et al., 1992), having been described only in *H. kigeziensis* Durette-Desset, Chabaud, Ashford, Butynski, and Reid, 1992.

Although specimens examined and redescribed by Travassos (1921) from Brazil appeared similar in all other major details to those from diverse regions, the length of the esophagus was markedly short (Table 3). The basis or significance of this difference in esophageal length of Travassos' (1921) specimens is unknown but could potentially indicate a lapse or, alternatively (but less likely), a regional isolation of this parasite in South America.

The broad morphological similarity of apparently disjunct populations of *H. rubidus* supports the concept of a widely distributed cosmopolitan species that has been disseminated extensively with the movement of domestic swine (e.g., to Australia [Pavlov, 1988] and North America). This may also be reflected in the relatively recent first reports of *H. rubidus* from Belgium in 1951, Japan in 1987, and South Africa in 1991 (Thoonen and Vercruysse, 1951; Sarashina and Taniyama, 1986; Boomker et al., 1991).

Validity of the genus *Cervicaprastrongylus*

Based on a comparison of the spicules, bursa, and genital cone of *H. rubidus* and details of

Table 3. Morphometrics (in micrometers; range with $\bar{x}$ and SD in parentheses) of females of *Hyostrongylus rubidus*.*

Characters	1	2	3	4	5	
Number examined	—	—	—	—	—	
Body length	8,000–8,500	5,300–8,000	8,000–9,000	4,800–8,000	7,340–9,360	(8,000)
Cephalic vesicle length	—	—	—	—	—	
Esophagus length	640	230–280	—	530–608	621–769	(700)
Esophagus as % of body length	7.5–8.0‡	3.5–5.3‡	—	7.6–11‡	8.2–8.5‡	
Esophageal–intestinal valve length	—	—	—	—	—	
Esophageal–intestinal valve width	—	—	—	—	—	
Subventral esophageal gland orifices§	—	—	—	—	—	
Excretory pore§	230–290	240	—	234–266	—	
Cervical papillae§	670	200	—	296–315	247–422	(352)
Vulva position§	—	4,350–6,500‡	6,300–7,100‡	3,880–6,628‡	6,080–6,628‡	(6,500)
% of body length to vulva	—	81–82‡	79‡	81–83	81–83‡	(81)
Anterior infundibulum length	—	—	—	—	—	
Posterior infundibulum length	—	—	—	—	—	
Anterior sphincter length‖	—	—	—	—	—	
Posterior sphincter length‖	—	—	—	—	—	
Ovejector length	—	—	—	—	—	
Tail length	680	100	200	129–152	—	

* 1 = Hassall and Stiles (1892), original description from natural infections in *Sus scrofa* from Washington, D.C. 2 = Travassos (1921), redescription of specimens in *Sus scrofa* from Brazil. 3 = Goodey (1924), redescription of specimens from naturally infected *Sus scrofa* from Great Britain. 4 = Alicata (1935), specimens from experimental infections in guinea pig (*Cavia porcellus*). 5 = Thoonen et al. (1951), redescription from natural infections in *Sus scrofa* in Belgium. 6 = Sprehn (1957). 7 = Sarashina and Taniyama (1986), redescription from natural infections in *Sus scrofa* in Hokkaido, Japan. 8 = Present study, redescription from natural infections in *Sus scrofa* and *Ovis aries* from North America and Central America.

† *n* for individual measurements.

‡ Calculated from numerical values in previous descriptions.

§ Measured from anterior.

‖ Measurements include the sphincter and vestibula as the muscular portion of the sphincter could not be clearly differentiated from the distal vestibula.

descriptions of those species currently referred to *Cervicaprastrongylus*, it is apparent that the latter genus cannot be reduced as a synonym of *Hyostrongylus*. The spicules characteristic of *C. gabonensis* (Durette-Desset and Chabaud, 1974), *C. moreli* (Durette-Desset and Denke, 1978), and *C. malviyai* (Chaturvedi and Kansal, 1977) (type for the genus) all have a dorsal and ventral process extending posteriad from the alae along the main shaft and a characteristic "eyelet" at the level of the trifurcation of the spicule tips (Durette-Desset and Chabaud, 1974; Durette-Desset and Denke, 1978; Gibbons and Khalil, 1982b). In contrast, spicules of *H. rubidus* are relatively simple (although trifurcate), being composed of a main shaft and slender ventral and dorsal processes extending posteriad from the alae; an eyelet is absent. In addition, most species of *Hyostrongylus* (exclusive of those referred to *Cervicaprastrongylus*) apparently have only a single prominent dorsal process on each spicule (but see Durette-Desset et al. [1992], who suggest it is necessary to confirm this by dissection). Although there is similarity in the 2–2–1 pattern of the bursa, the structure of the dorsal ray may differ in the location and number of lateral processes and in position of the bifurcation (see Trach, 1986; Govorka et al., 1988). Additionally, the simple, rectangular accessory bursal membrane, supported by 2 widely separated dorsal raylets (#7 papillae), differs from that in species of the genus *Cervicaprastrongylus* (Gibbons and Khalil, 1982b; Trach, 1986). However, placement of both genera in the Ostertagiinae is supported by the presence of paired "0" papillae on the ventral aspect of the genital cone (see Hoberg and Lichtenfels, 1992; Lichtenfels and Hoberg, 1992).

Recognition of *Cervicaprastrongylus* and *Hyostrongylus* requires comment on the species referred to these genera. In addition to *H. rubidus*, 5 other species of *Hyostrongylus* have been recognized including *H. okapiae* (Van den Berghe, 1937) from *Okapiae johnstoni* (Sclater) in central

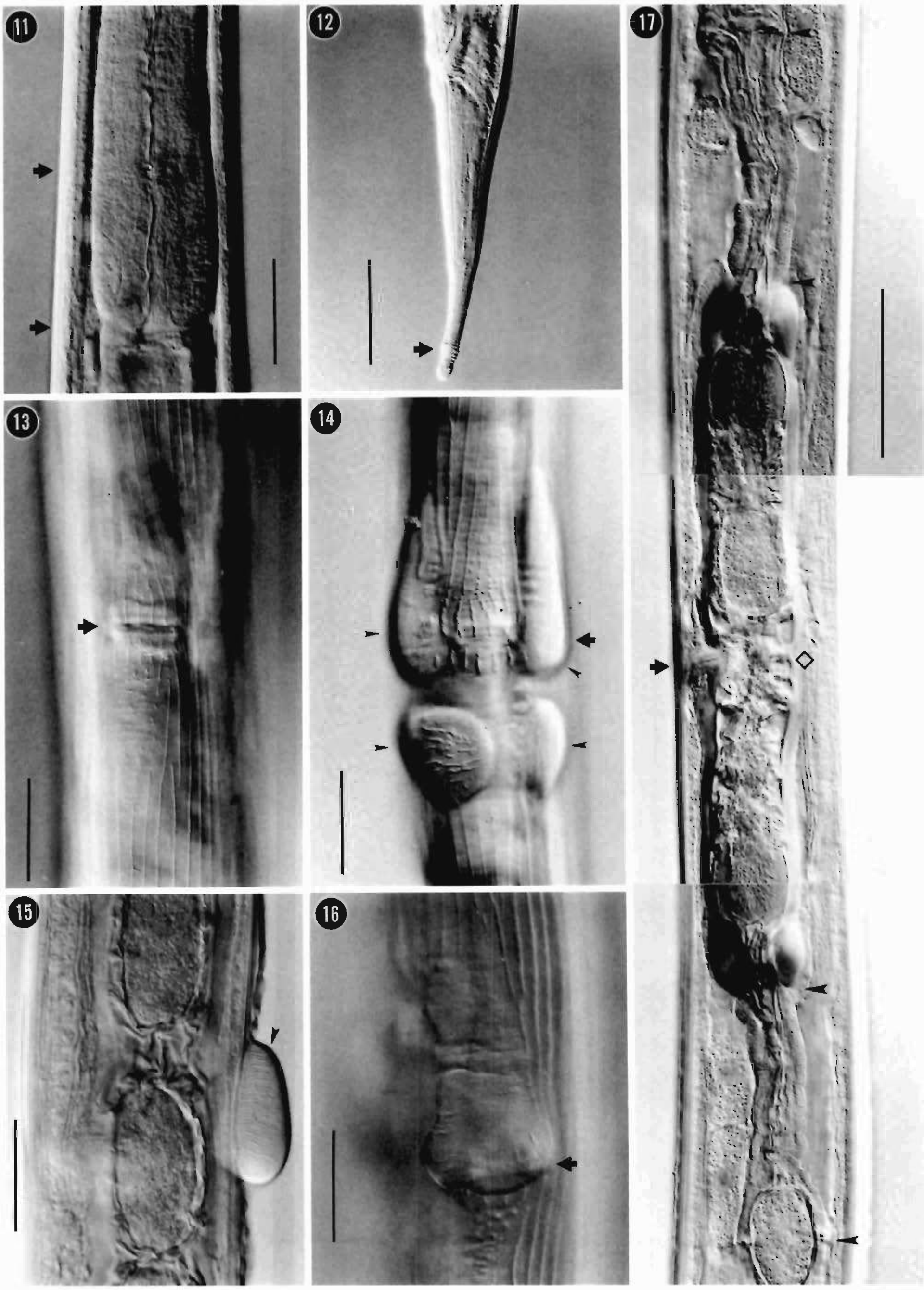
Table 3. Continued.

6	7		8		
—	20			50	
5,000–10,000	7,396–8,796	(8,070)	[50]†	4,554–10,275	(7,574 ± 1,274.2)
	—	—	[46]	57–88	(69 ± 6.76)
660–750	640–807	(713)	[50]	570–770	(677 ± 47.11)
7.5–13.2‡	8.6–9.2‡	(8.8)	[50]	7–13	(9.13 ± 1.3)
—	—	—	[49]	57–86	(71 ± 7.17)
—	—	—	[49]	36–57	(49 ± 6.23)
—	—		[47]	237–328	(278 ± 23.47)
240	226–357	(287)	[48]	244–403	(323 ± 44.23)
400–670	231–376	(306)	[48]	248–433	(344 ± 47.16)
—	6,284–7,241‡	(6,773)	[50]	3,883–8,600	(6,265 ± 1,085.43)
—	82–85‡	(84)	[50]	77–85	(83 ± 1.46)
—	—	—	[39]	94–161	(127 ± 15.2)
—	—	—	[40]	73–151	(115 ± 15.91)
—	—	—	[44]	99–255	(171 ± 41.89)
—	—	—	[44]	88–225	(149 ± 34.67)
—	—	—	[39]	413–735	(566 ± 86.89)
68–100	118–157	(140)	[45]	104–174	(142 ± 16.77)

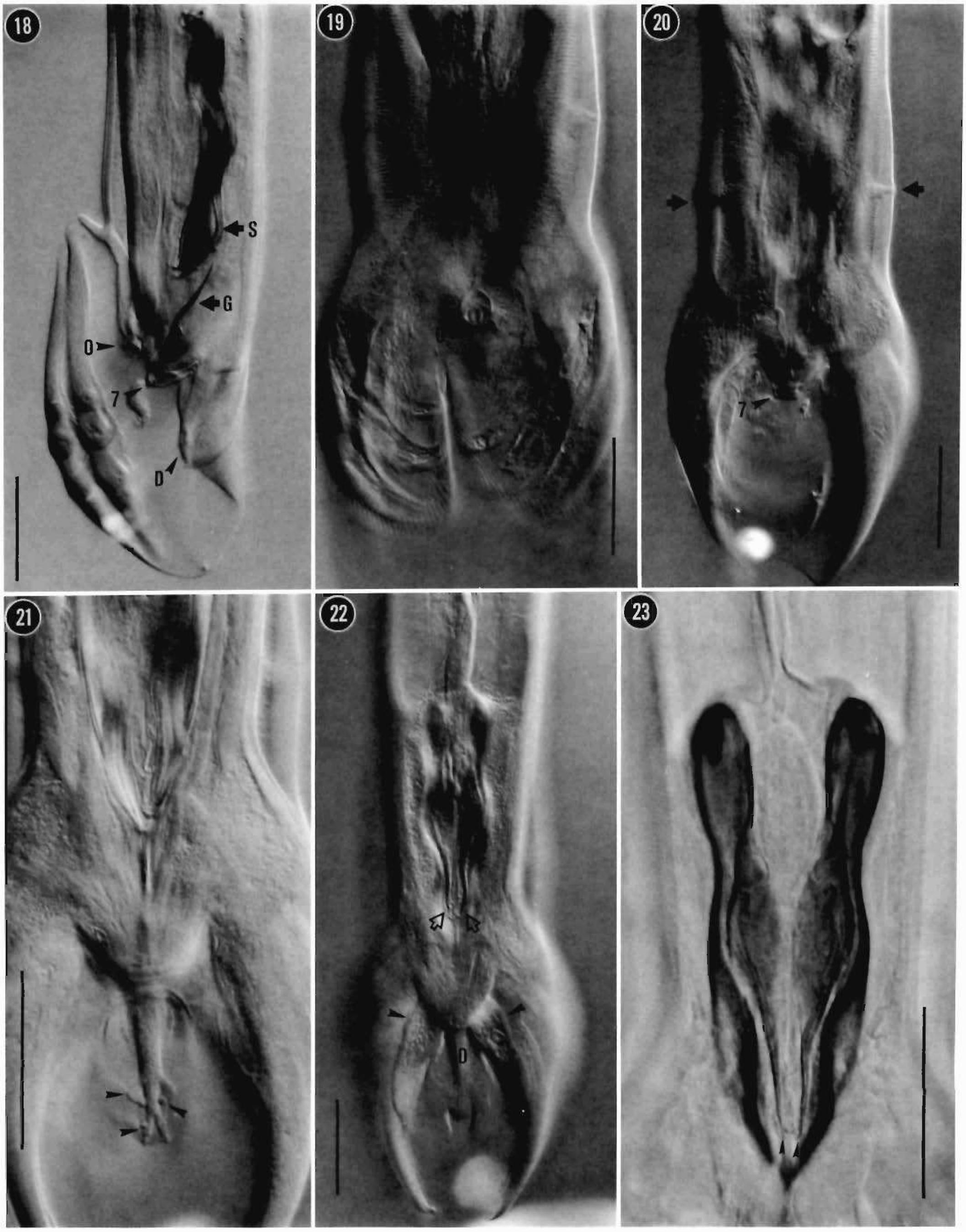
Africa, *H. vinnica* Trach, 1986, from sheep and cattle in the Ukraine, *H. gabonensis* from the tragulid *Hyemoschus aquaticus* Ogilby in Gabon, *H. moreli* from the leporid *Lepus capensis* Linnaeus in Mali, and *H. kigeziensis* from *Gorilla gorilla* (Savage and Wyman) in Uganda (Durette-Desset and Chabaud, 1974; Durette-Desset and Denke, 1978; Trach, 1986; Durette-Desset et al., 1992). *Hyostrongylus gabonensis* and *H. moreli* were subsequently transferred to the Ostertagiinae when *Cervicaprastrongylus* Gibbons and Khalil, 1982, was established for several trichostrongylids from lagomorphs and ruminants (Gibbons and Khalil, 1982b). The validity of this genus has been questioned by Jansen (1989) and Durette-Desset et al. (1992), who considered it to be a synonym of *Hyostrongylus*. The concepts of Gibbons and Khalil (1982a, b) would refer 4 species to *Hyostrongylus* and 3 to *Cervicaprastrongylus* and relegate both genera to the Ostertagiinae, whereas Durette-Desset et al. (1992) would refer 7 species (if *H. vinnica* is included) to the former genus and apparently (based on exclusion from the Ostertagiinae) place them in the Graphidiinae.

Referral of *Hyostrongylus* to the Ostertagiinae

Recent studies of the Trichostrongylidae have referred *Hyostrongylus* to the Ostertagiinae (Gibbons and Khalil, 1982a; Trach, 1986; Jansen, 1989), although Durette-Desset and Chabaud (1977, 1981) and Durette-Desset (1983, 1985, 1989) placed this genus among the Graphidiinae. The presence of paired "0" papillae (raylets) on the ventral aspect of the genital cone in *H. rubidus* supports placement of the genus in the Ostertagiinae. In this regard, Chabaud et al. (1970) considered that the minuscule paired "0" papillae of many rhabditea represented the ancestral condition for these nematodes. However, fusion of these papillae is typical of the Strongyloidea, Ancylostomatoidea, Metastrongyloidea, and all Trichostrongyloidea except the members of the Ostertagiinae. Hypertrophy of these papillae among the Ostertagiinae is substantial, such that they are definably different from the putative ancestral condition. Consequently, within the context of outgroup comparison with all other strongylates, the paired ventral raylets of the Ostertagiinae represent a putative synapomorphy for the subfamily (see Hoberg and Lichtenfels, 1992; Lichtenfels and Hoberg, 1993) and are uniformly present only among *Hyostrongylus* and those genera collectively referred to the Ostertagiinae by Durette-Desset (1983, 1989), Gibbons and Khalil (1982a, 1983), and Jansen (1989). Additional characters that may support placement in the Ostertagiinae include relatively short spicules, irregular cuticular inflations at the level



Figures 11–17. **Esophageal, cuticular and internal characters of females of *Hyostrongylus rubidus*. Scale bars = 50 μm for Figures 11–16 and 100 μm for Figure 17. 11. Esophageal valve (between arrows) showing typical structure and relatively short length. 12. Tail showing usual cuticular rings at tip (arrow). 13. Vulva in ventral view (arrow) showing simple structure in the vulval region without prominent cuticular inflations. 14. Vulva in ventral view (arrow) showing 4 complex and prominent cuticular inflations (pointers), each formed by hypertrophy of several ridges, and irregular pattern of synlophe in the vulval region. 15. Single lateral inflation near the level of the vulva (pointer). 16. Flap-like structure covering vulva (arrow). 17. Ovejectors (anterior directed toward top of figure) showing position of vulva (arrow) anterior and posterior vestibula and sphincters (between diamond and pointers) and the anterior and posterior infundibula (between pointers); note absence of cuticular modification at level of vulva in this specimen.**



Figures 18–23. Characters of male specimens of *Hyostrongylus rubidus*. Scale bars = 50 μm. 18. Lateral view of the genital cone showing position of "0" papillae (0), "7" papillae (7), dorsal lobe with dorsal ray (D), gubernaculum (G), and dorsal process of spicule tips (S). 19. Ventral view of bursa showing position and structure of the paired "0" papillae (0). 20. Ventral view of bursa showing position and structure of "7" papillae (7) and the position of the prebursal papillae (arrows). 21. Dorsal view of bursa showing configuration of the dorsal ray with 2 pairs of laterally directed processes anterior to the bifurcation from which additional processes arise (pointers). 22. Dorsal view of bursa showing dorsal position of externodorsal rays (pointers) with respect to the dorsal lobe and dorsal ray (D); note also the elongate dorsal processes of the spicules (arrows). 23. Spicules, dorsal view, showing prominent dorsal processes extending from the dorsal alae.

of the vulva (Hoberg and Lichtenfels, 1992; Hoberg et al., 1993b), and a 2–2–1 bursa.

Comparisons among other Ostertagiinae in which the synlophe and genital cone have been evaluated indicate the need for critical assessment of these and other characters (e.g., esophageal valve) in developing a concept for relationships within the subfamily. Considering species with a 2–1–2 bursa, 2 forms of the lateral synlophe are recognized. Some species of *Ostertagia* (*O. ostertagi* (Stiles, 1892) and *O. bisonis* Chapin, 1925 and associated minor morphotypes), *Longistrongylus* (*L. sabie* (Mönnig, 1932) and *L. curvispiculum* (Gibbons, 1973)), and *Camelostrongylus mentulatus* (Railliet and Henry 1909) have a tapering cervical synlophe (largely definable as the Type I pattern of Lichtenfels et al. [1988]). A parallel cervical synlophe (Type II pattern of Lichtenfels et al. [1988]) is present in *Ostertagia leptospicularis* Assadov, 1953, *O. gruehneri* Skrjabin, 1929, *O. mossi* Dikmans, 1931, and *Marshallagia marshalli* (Ransom, 1907) and the putative minor morphotypes associated with these species (Hoberg et al., 1993a). In contrast, among those species known to have a 2–2–1 bursa (species of *Teladorsagia* Andreeva and Satubaldin, 1954, *Spiculopteragia* (Orloff, 1933), and *Mazamastrongylus* Cameron, 1935), the synlophe has a tapering pattern laterally in the cervical zone (Type I of Lichtenfels et al. [1988] is definable only in *Teladorsagia*). However, the form of the bursa is 2–2–1 in *H. rubidus*, and although the lateral synlophe has 5 continuous parallel ridges the Type II lateral pattern (3–5 narrowly spaced parallel ridges in each lateral field) is absent. The cervical synlophe of *H. rubidus* differs in having a constant interval between ridges. The presence of a 2–2–1 bursa and a parallel synlophe constitute a combination of characters not compatible with the patterns defined for some of the genera and species already outlined. Elucidation of the relationships of these and other genera referred to the Ostertagiinae thus requires development of explicit hypotheses for homology for elements of the synlophe and genital cone along with the definition of character-state transformation series.

Relationship of the Ostertagiinae and Graphidiinae

Recognition of *Hyostrongylus* and the species currently referred to *Cervicaprastrongylus* within the Ostertagiinae (Gibbons and Khalil, 1982a) requires reconsideration of hypotheses for multiple origins of the former subfamily from the Graphidiinae (Durette-Desset and Chabaud, 1977, 1988; Durette-Desset, 1983, 1985). Whether or not *Hyostrongylus* is basal within the Ostertagiinae remains to be determined. However, there is a parallel synlophe that is unmodified, a relatively high number of ridges, and a 2–2–1 bursa. In contrast, the Graphidiinae (according to Gibbons and Khalil [1982a], and with the removal of *Hyostrongylus* sensu Durette-Desset et al. [1992] and *Parostertagia* Schwartz and Alicata, 1933) would be defined by a 2–1–2 bursa (rather than 2–2–1 and 2–1–2) and an unmodified parallel synlophe (Hoberg and Lichtenfels, 1992). Both of these characters are widespread within the Molineidae (see Durette-Desset 1983, 1985) and, thus (by outgroup comparison), may constitute the plesiomorphic condition with respect to the Graphidiinae and Ostertagiinae and as such are not phylogenetically informative. With an unmodified parallel synlophe as plesiomorphic, Type II and Type I patterns would be derived within the Ostertagiinae. Additionally, the 2–2–1 pattern of the bursa appears to be limited to the Ostertagiinae (within the Trichostrongylidae) and a few distantly related heligmosomes (Durette-Desset, 1983, 1985). These latter characters of the synlophe and bursa along with the paired "0" papillae are postulated as apomorphic within the Ostertagiinae, with the latter attribute representing a putative synapomorphy for the subfamily, as presented earlier. *Hyostrongylus* could thus be basal within the Ostertagiinae. However, the relationship for *Hyostrongylus* as the basal member of a more inclusive group within the Ostertagiinae continues to require confirmation, as indicated by previous workers (Dróżdż, 1965, 1967; Durette-Desset and Chabaud, 1977, 1981; Durette-Desset, 1982, 1983, 1985; Jansen, 1989).

Durette-Desset and Chabaud (1977, 1981) in their classic essays on the classification of the Trichostrongyloidea proposed multiple origins for the Ostertagiinae from 2 genera of the Graphidiinae. *Hyostrongylus* (within the Graphidiinae) was considered the basal member of a lineage that included 3 genera of the Ostertagiinae with a 2–2–1 bursa: *Spiculopteragia* (Orloff, 1933), *Teladorsagia* Andreeva and Satubaldin, 1934, and *Gazellostrongylus* Yeh, 1956 (the latter now referred by Durette-Desset [1983] to the Cooperiinae). Jansen (1989) also included *Mazamastrongylus* Cameron, 1935, with those genera postulated as being derived from a *Hyostron-*

gylus-like trichostrongylid. Concurrently, *Graphidium* Railliet and Henry, 1909, was postulated as the basal member of a lineage of 3 other genera of ostertagiines with a 2–1–2 bursa: *Marshallagia* (Orloff, 1933), *Longistrongylus* (Le Roux, 1931), and *Ostertagia* Ransom, 1907. If this view is correct, then it would become necessary to synonymize the Ostertagiinae and Graphidiinae. Otherwise, in the currently accepted classification of the Trichostrongyloidea (Durette-Desset, 1983, 1985), the Ostertagiinae would be polyphyletic (derived independently from 1 or more ancestors referred to another taxon), whereas the Graphidiinae would become paraphyletic (a taxon with a common ancestor, but with exclusion of 1 or more descendants) (Hennig, 1966; Wiley, 1981; Wiley et al., 1991). In either case, these taxa would be artificial with a resulting classification (cladistic or otherwise) being inconsistent with the phylogenetic history of these trichostrongylid subfamilies (see opinions on classification in Khalil and Gibbons, 1981; Jansen, 1989).

However, recognition of an unequivocal synapomorphy defining the Ostertagiinae (to the exclusion of the Graphidiinae) refutes the hypothesis for multiple origins. Alternative hypotheses suggest that (1) the Ostertagiinae and Graphidiinae may be sister-groups (sharing a common ancestor; also refuted by absence of a synapomorphy for both subfamilies) or (2) the Ostertagiinae and Graphidiinae are more closely related to other subfamilies of Trichostrongylidae. Although monophyly appears established for the Ostertagiinae, any putative relationship with the Graphidiinae or other subfamilies of the Trichostrongylidae must yet be clarified within the context of phylogenetic analyses of the family currently in progress.

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Meeting Schedule

HELMINTHOLOGICAL SOCIETY OF WASHINGTON
1993–1994

(Wednesday) 6 October 1993	Anniversary Dinner Meeting hosted by the Uniformed Services University of the Health Sciences. Time and place to be announced.
(Wednesday) 10 November 1993	National Institutes of Health, Bethesda, MD
(Wednesday) 6 February 1994	Animal Parasitology Unit, U.S. Department of Agriculture, Beltsville, MD
(Wednesday) 6 April 1994	Johns Hopkins University, Baltimore, MD
(Saturday) 7 May 1994	Joint Meeting with the New Jersey Society for Parasitology, at the New Bolton Center, University of Pennsylvania, Kennett Square, PA